Influence of Prescribed Fire on Carabid Beetle (Carabidae) and Spider (Araneae) Assemblages in Forest Litter in Southwestern Oregon

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ABSTRACT   The objective of this study was to determine if prescribed fire affects spider (Araneae) and carabid beetle (Carabidae) abundance, and whether the magnitude of this effect varies with time since fire. Within mixed conifer stands, nine understory fuels-reduction burns, ranging from <1 to 15 yr old, were compared with adjacent unburned sites. Pitfall traps were used to compare macroarthropod abundance over 5 mo. In total, 3,441 spiders in 24 families and >120 species, and 14,793 carabid beetles from 17 species, were identified from the samples. Seven spider families and five species of carabid beetles were abundant enough to be analyzed statistically. Four spider families were more abundant in unburned sites (Antrodiaetidae, Cybaeidae, Thomisidae and Linyphiidae) while three families were more numerous in burned sites (Lycosidae, Gnaphosidae and Dictynidae). Four of five carabid beetle species were more abundant in unburned sites [*Pterostichus herculaneus* Mannerheim, *P. setosus* Hatch, *Scaphinotus rugiceps rugiceps* (Horn) and *Zacotus matthewsii* LeConte]. There was no difference found for *Omus cazieri* van den Berghe. No differences in species richness or diversity (Simpson, Shannon-Wiener and Berger-Parker indices) were found for spiders or carabid beetles. Overall, the relationship between abundance and time since burning was weak, with marginal significance found only for Dictynidae and Gnaphosidae. We suggest that changes in foraging substrate, prey availability or microclimatic conditions since fire may have interacted with life history characteristics to influence the abundance of these organisms. Differences in fire intensities among years may have masked patterns in arthropod abundance associated with time since burning.

KEY WORDS   prescribed fire, forest litter arthropods, spiders, Carabidae, Oregon, pitfall traps

FIRE IS A major factor influencing the composition and structure of forests in the Pacific Northwest (Agee 1993). In southwestern Oregon, where summers are typically hot and dry, wildfires historically are frequent; average fire return intervals as short as 20 yr have occurred over much inland coniferous forest in this region (Atzet and Wheeler 1982). These wildfires were generally of light intensity, and occasionally fires would burn large areas, destroying much timber. To prevent this loss of wood resources, fire suppression was initiated in the early 1900s. In the absence of fire, however, major changes in the structure of forests occurred in many areas. These changes include an increase in the density of tree species less tolerant of fire (McNeil and Zobel 1980) and unnaturally high accumulations of both downed and standing dead wood (Parsons and DeBenedetti 1979). As a result of this greater fuel load, the chance of high intensity, catastrophic wildfire has increased. To minimize this risk, controlled understory burning has been introduced as a management strategy to reduce fuel loads

on many forests. Although prescribed fire can be effective at obtaining this goal, it carries the possibility of greatly modifying the structure of the habitat for understory arthropod communities. The effect of prescribed fire on arthropod communities, and the ecological processes they influence, is poorly understood.

A variety of studies have investigated the effect of fire on forest arthropod communities. Most have looked at either the influence of stand-replacing wildfire (Harris and Whitcomb 1974, Richardson and Holliday 1982, Holliday 1992) or prescribed fire as a site preparation measure (e.g., slash burning) following timber harvest (Huhta 1971, Neumann 1991, Beaudry et al. 1997). Fewer studies have looked at the effect of prescribed underburning on litter arthropod communities. In the Jarrah forests of western Australia, both Majer (1984) and Abbott (1984) found no difference in total arthropod abundance between burned and unburned sites immediately after prescribed fire, although abundances were lower in burned sites for some taxa. Among South Carolina longleaf pine stands burned ≈1, 2, and 3 yr before sampling, New and Hanula (1998) also found no difference in total litter

arthropod abundance, but spiders were more numerous in stands burned 3 yr previously than in those burned 2 yr prior. Results from these studies suggest that the abundance of some forest litter arthropods may be reduced following prescribed fire, but the longer-term response is unclear.

The primary goal of this research was to determine the short- and longer-term effects of prescribed understory fuels reduction burning on litter macroarthropod communities within a managed forest ecosystem in southwestern Oregon. We hypothesized that fire would have an initial impact on the abundance of many arthropod taxa, but that the arthropod community in burned areas would become increasingly similar to those in unburned areas as time since fire increased. We focused on carabid beetles (Carabidae) and spiders (Araneae) for the following reasons: (1) they are abundant and diverse in forest ecosystems; (2) they have a long history of use in ecological studies, many of which used pitfall traps to quantify relative activity or abundance (Thiele 1977, Wise 1993); (3) most common species are relatively easy to identify; (4) many are known to be sensitive to changes in habitat structure (Thiele 1977, Uetz 1979); (5) they use a variety of feeding modes, with some being specialists and some generalists (Thiele 1977, Wise 1993); and (6) both have been cited as taxa potentially useful as indicators of environmental disturbance (McIver et al. 1992, Beaudry et al. 1997).

Materials and Methods

Study Area. This study took place within the Ashland watershed, ≈6.4 km south of Ashland, OR, in the Ashland Ranger District, Rogue River National Forest. Ranging from 900 to 1,500 m elevation, this area of the Klamath Mountains of southwest Oregon is represented by white fir [*Abies concolor* (Gord. & Glend) Lindl. ex Hildebr.] and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] climax forest zones. The distribution and elevational range of forest zones in this area are greatly influenced by local geomorphological and climatic conditions; however, in general the white fir zone averages 1,300 m in elevation and the Douglas-fir zone averages 850 m in elevation (Atzet et al. 1996). Under natural fire regimes, these forests would consist of a mixed assemblage of conifers, dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and Douglas-fir. They also would include white fir and sugar pine (*Pinus lambertiana* Dougl.), and would be multistoried and relatively open, containing little coarse wood debris. However, fire suppression has resulted in many sites becoming densely stocked with sapling and pole-sized white fir and Douglas-fir, and with a large accumulation of standing and down dead wood.

Within the watershed, nine understory fuel reduction prescribed burns performed between 1983 and 1998 met criteria for inclusion in the study. Burn years were as follows: 1983, 1986, 1991, 1993, 1994, 1995, 1996, 1997, and 1998. Criteria evaluated for inclusion were as follows: (1) the site was dominated by Dou-

glas-fir (>50% canopy cover); (2) the site had not experienced confounding events, such as thinning, compaction, or having been burned on more than one occasion, and; (3) the site could be matched with an adjacent or nearby unburned control site, with similar aspect, elevation, forest structure and recent history. Locating acceptable control sites was critical due to differences in forest structure inherent to the varied landscape. Fires were located using GIS maps provided by personnel at the Rogue River NF, Ashland, OR. The perimeter of each fire was determined by locating fire scars on tree trunks. All nine prescribed fires were conducted during spring months. The prescribed burn that took place during the year of the study (1998) was performed over two time periods; 8–9 June and 19 June 1998. The second burn was required due to poor initial burn conditions and concerns for air quality in the nearby town of Ashland.

Arthropod Sampling. During 1998, arthropods were collected using pitfall traps. Pitfall traps consisted of a 2-liter plastic bucket (14-cm-diameter opening) fitted with a metal funnel and covered with a 25 by 25-cm plastic rain cover suspended with nails 5 cm above the trap. Trap buckets were buried in the ground with their tops placed flush with the level of the forest floor. A 250-ml glass canning jar partially filled with ethylene glycol (50% solution) was placed beneath each funnel to catch and preserve arthropods falling into the traps. Within each of the 18 sites, 12 pitfall traps were placed at 30-m intervals along transects. Transects ran along terrain contours and were placed no closer than 30 m from a site boundary.

Pitfall traps at all sites except the 1998 and 1995 burns were run for seven 2-wk (approximately) intervals: one interval in the late spring (3 June–17 June); two intervals in the late spring/early summer (17 June–8 July and eight July–21 July), two in midsummer (4 August–18 August and 18 August–1 September), and two in the late summer/early fall (15 September–29 September and 29 September–13 October). The gap between sampling periods was designed to reduce trapping pressure on the litter arthropod community. Because it was not known on what date burning would take place, sampling before the burn was not possible; traps in the 1998 burn site were installed on 18 June in the portion of the site that burned 8–9 June. Traps were not placed in the 1995 burn until 1 July because of uncertainty of the availability of the site. For traps in the 1998 and 1995 sites, retrieval of catches began on the first collection date following their placement. All adult carabid beetles and spiders were identified to the species or morphospecies level. Voucher material was deposited in the USFS Western Forest Insect Collection (Oregon State University, Corvallis, OR). In addition to carabid beetles and spiders, the following major arthropod taxa were considered to be potential prey or competitors, and were counted and analyzed: Chilopoda; Diplopoda; Formicidae; holometabolous insect larvae; Opiliones; Orthoptera; and Thysanura.

Litter Biomass. Within each site, 16 litter samples (10 by 10 cm) were collected, 20 m apart, along the

Table 1. Total carabid beetles trapped and mean ± SE abundance, species richness and diversity in nine paired burned and unburned sites

Species[a]	Total no. trapped	Burned	Unburned
Amara conflata LeConte	114	7.4 ± 2.1	5.3 ± 1.7
Cychrus tuberculatus Harris	9	0.6 ± 0.4	0.4 ± 0.3
Harpalus cautus Dejean	23	2.3 ± 1.3	0.2 ± 0.2
Metrius contractus contractus Escholtz	15	1.2 ± 0.7	0.4 ± 0.4
Notiophilus directus Casey	13	1.3 ± 0.4	0.1 ± 0.1
Omus cazieri van den Berghe	3,678	199.7 ± 57.5	209.0 ± 75.0
Pterostichus herculaneus Mannerheim	1,313	46.3 ± 11.9	99.6 ± 23.6
Pterostichus lama Menetries	102	5.2 ± 1.2	6.1 ± 1.8
Pterostichus melanarius (Illiger)	5	0.2 ± 0.2	0.3 ± 0.2
Pterostichus setosus Hatch	6,277	171.0 ± 108.0	526.4 ± 275.6
Scaphinotus rugiceps rugiceps (Horn)	2,655	105.4 ± 34.9	189.6 ± 61.6
Trachypachus holmbergi Mannerheim	26	2.9 ± 2.9	0.0 ± 0.0
Zacotus matthewsii LeConte	559	9.7 ± 5.0	52.4 ± 13.9
Total Carabidae	14,793	553.6 ± 196.9	1,090.1 ± 350.0
Species richness (S)		8.4 ± 0.6	7.4 ± 0.5
Simpson Index (1-D)		0.6 ± 0.1	0.7 ± 0.1
Berger-Parker Index (1/d)		2.1 ± 0.2	2.1 ± 0.2
Shannon-Wiener (H′)		1.0 ± 0.1	1.1 ± 0.1

[a] Species represented by a single specimen: *Amara littoralis* Mannerheim; *Bembidion erasum* LeConte; *Dicheirus piceus* (Menetries) and *Harpalus fuscipalpis* Sturm.

transects on which pitfall traps were placed. Because the samples were part of a study involving microarthropods, every four consecutive samples were combined in the laboratory for microarthropod extraction using Berlese-style funnels. After extraction, each sample was lightly washed to remove rocks, soil, cones and sticks larger than 0.75 cm diameter, air-dried and weighed. Because litter depth was difficult to measure accurately, biomass was used as an estimator of litter development.

Statistical Analysis. Before analysis, count data from individual pitfall traps were summed together within each site on each date. These totals were then standardized as the number of individuals/10 traps/100 trap days. Standardization was necessary because of an uneven number of traps within a sample period due to loss from wildlife and because the number of days in the first sample period differed from the other sample periods. Within a site, each standardized value was then pooled within a sampling date for analysis. Because replication was at the site level (nine paired sites), this single value for each site was used in the analysis. Only taxa comprising >3% of the total catch were considered abundant enough to analyze statistically (Gauch 1982, Weaver 1995). Analyses were performed at the species level for carabid beetles and the family level for spiders.

The effect of prescribed fire on the carabid beetle and spider fauna was analyzed using Poisson log-linear multiple regression models (MathSoft 1999). This statistical method was used because the assumptions for analysis with the normal distribution were not met and standard transformations did not stabilize the variance. There was a large amount of extra-Poisson variation in the data so the quasi-likelihood approach was used to provide *P* values adjusted for this variation. Explanatory variables included in the models were treatment (burned versus unburned), years since burn (0, 1, 2, 3, 4, 5, 7, 12, and 15 yr), sampling date (used as a blocking factor), and litter weight. Interactions among the explanatory variables were also examined.

Three measurements of species diversity widely used in ecological studies were calculated to describe the pattern of carabid beetle and spider abundance from each site: the Simpson index, the Berger-Parker index, and the Shannon-Wiener index (Magurran 1988). The Simpson index (Simpson 1949) and Berger-Parker index (Berger and Parker 1970) are both dominance measurements, weighting toward the most abundant species, rather than emphasizing species richness. The Shannon-Wiener index (H′) is more sensitive to rare species and overall species richness than it is to dominance of one or a few species (Krebs 1989). Wilcoxon's signed-ranks tests for paired groups were used to compare species richness and diversity indices between burned and unburned sites (Sokal and Rohlf 1981).

Wilcoxon's signed-ranks tests for paired sites were also used to evaluate whether differences existed between burned and unburned sites among arthropods other than carabid beetles and spiders, and for litter biomass. The comparison for each of these arthropod groups was based upon the average number of individuals collected within each site over the course of the study.

Results

Carabid Beetles. A total of 14,793 carabid beetles, representing 17 species, was collected over the course of the study (Table 1). *Pterostichus setosus* Hatch was the most abundant species, comprising 42.4% of the total, followed by *Omus cazieri* van den Burgh (24.9%), *Scaphinotus rugiceps rugiceps* (Horn) (18.0%), *Pterosticus herculaneus* Mannerheim (8.9%), and *Zacotus matthewsii* LeConte (3.8%); these five species were analyzed statistically. Twelve species
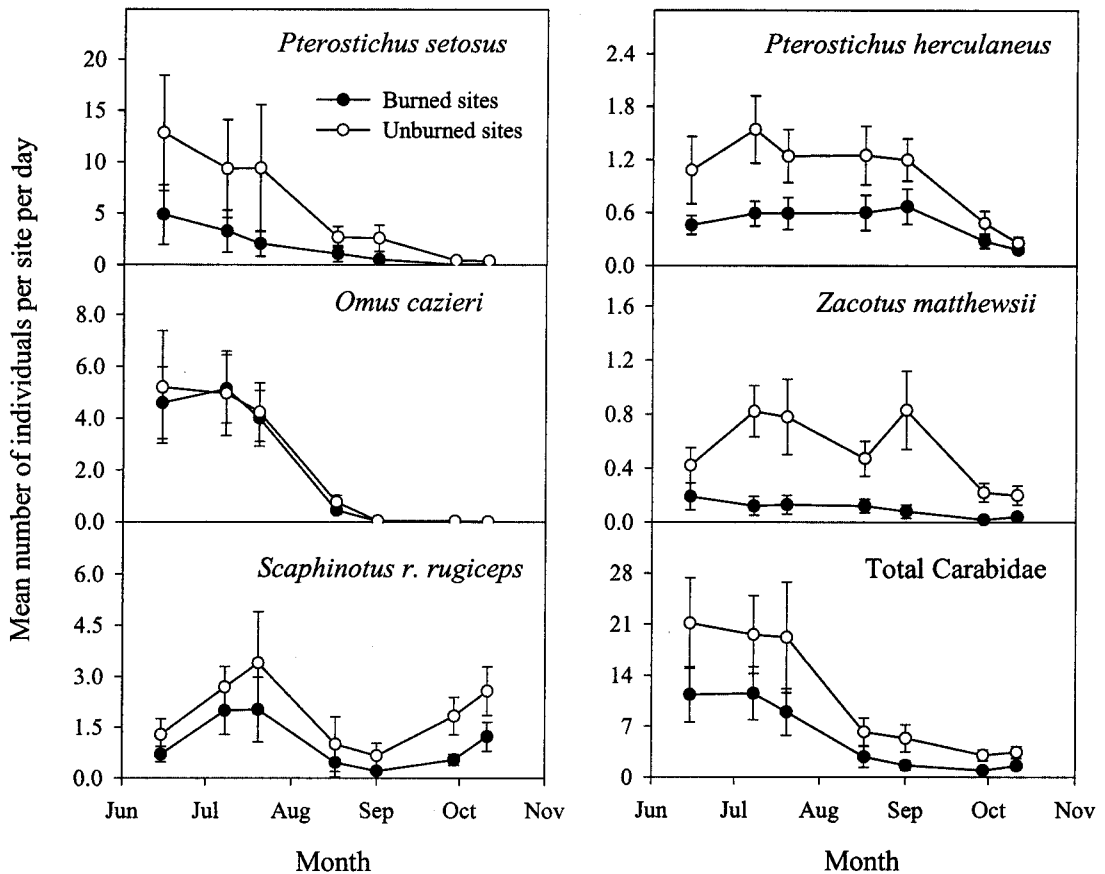
Fig. 1. Mean numbers ($\pm$SE) of the five most abundant species of carabid beetles, and the total number of Carabidae, in burned and unburned sites on seven sampling dates in 1998 ($n = 9$).

comprised the remaining 2.0% of the total, with the 10 least abundant species making up <1%. Overall, 66.3% of all individuals were collected in unburned sites. Species richness and diversity indices for carabid beetles were similar between burned and unburned sites (Table 1). No significant difference between treatments was found for species richness or any of the diversity indices ($P > 0.10$).

Temporal patterns of abundance varied among species over the season, but were generally similar within a species between burned and unburned sites (Fig. 1). Overall, a majority of the beetles was collected early in the season, with 80.1% of all individuals recovered during the first three sampling dates. For *O. cazieri*, *P. setosus*, and *P. herculaneus* the number of individuals caught decreased as the season progressed. In contrast, two periods of higher activity were found for *S. r. rugiceps*. The activity pattern was mixed for *Z. matthewsii*; its abundance decreased continuously throughout the season in burned sites but was bimodal in unburned sites.

For all taxa, the final Poisson regression model consisted of the variables: (1) treatment (unburned versus burned); (2) the interaction between treatment and time since burning; and (3) sample dates. Results

were similar for most species with significantly more individuals collected in unburned than in burned sites (Table 2). For *O. cazieri*, however, no significant difference was found between treatments.

If fire initially changed carabid beetle abundance, but beetles later returned to the level of the unburned sites, then the observed abundance pattern would be one which starts with an initial, relatively high, positive or negative value and decreases toward zero with increasing time since fire. A horizontal line would suggest no difference between unburned and burned sites with time. For only *O. cazieri* was a significant interaction found between abundance and time since burning (Table 2). Fig. 2 suggests that the abundance of *O. cazieri* was higher in burned sites early after fire, followed by an overall increase in unburned sites with increasing time since fire. Although the relationship was statistically significant ($P = 0.043$), variation among years was large, and the pattern does not strongly suggest that prescribed fire was a factor influencing decreasing differences between unburned and burned sites. In fact, little difference was found between sites for any of the four youngest burns. Overall, no consistent patterns were found for any of the taxa analyzed. While not analyzed statistically,

Table 2.   Poisson log-linear regression analyses comparing abundances of the five most common carabid beetles and total Carabidae in burned and unburned sites

Species	Residual deviance	Burned vs Unburned						Treatment × Time since burning interaction					
		Beta	SE	F	df	P	Direction[a]	Beta	SE	F	df	P	Direction[a]
Omus cazieri	13,355.4	NA	NA	0.14	1, 113	0.707	None	0.060	0.029	4.20	1, 112	0.043	Unburned
Pterosticus herculaneus	4,117.5	0.728	0.150	25.69	1, 113	<0.001	Unburned	−0.004	0.031	0.02	1, 106	0.894	None
Pterosticus setosus	55,783.9	1.171	0.311	20.32	1, 113	<0.001	Unburned	0.051	0.085	0.45	1, 106	0.505	None
Scaphinotus r. rugiceps	16,899.3	0.631	0.235	9.74	1, 113	0.002	Unburned	0.038	0.047	0.87	1, 106	0.352	None
Zacotus matthewsii	3,662.9	1.708	0.269	53.06	1, 114	<0.001	Unburned	0.027	0.058	0.20	1, 106	0.657	None
Total Carabidae	60,858.6	0.700	0.182	17.80	1, 114	<0.001	Unburned	0.019	0.039	0.26	1, 106	0.608	None

A significant interaction between treatment and time since burning indicates that an abundance pattern differed with increasing time since burning.

NA, Value not available because the variable was not significant in the final model.

[a] Refers to the treatment having the greatest abundance with increasing time since fire.

neither species richness or Simpson's index for carabids showed a distinct trend with time since burning (Fig. 3).

Spiders. A total of 3,441 adult spiders, representing 24 families, 73 genera, and >120 species, was collected over the course of the study (Table 3). The largest numbers of individuals were in the family Gnaphosidae (531), followed by Antrodiaetidae (520),

Thomisidae (472), and Dictynidae (440). Relatively few species dominated the samples numerically, with nine species comprising 59.4% of all individuals collected: *Blabomma* new sp. (12.2%); *Xysticus pretiosus* Gertsch (9.8%); *Atypoides gertschi* Coyle (8.1%); *Alopecosa kochii* (Keyserling) (6.9%); *Cybaeus* new sp. #3 (6.2%); and *Zelotes* near *viola* Platnick and Shadab (5.4%). Many species were rarely captured; 105 spe-
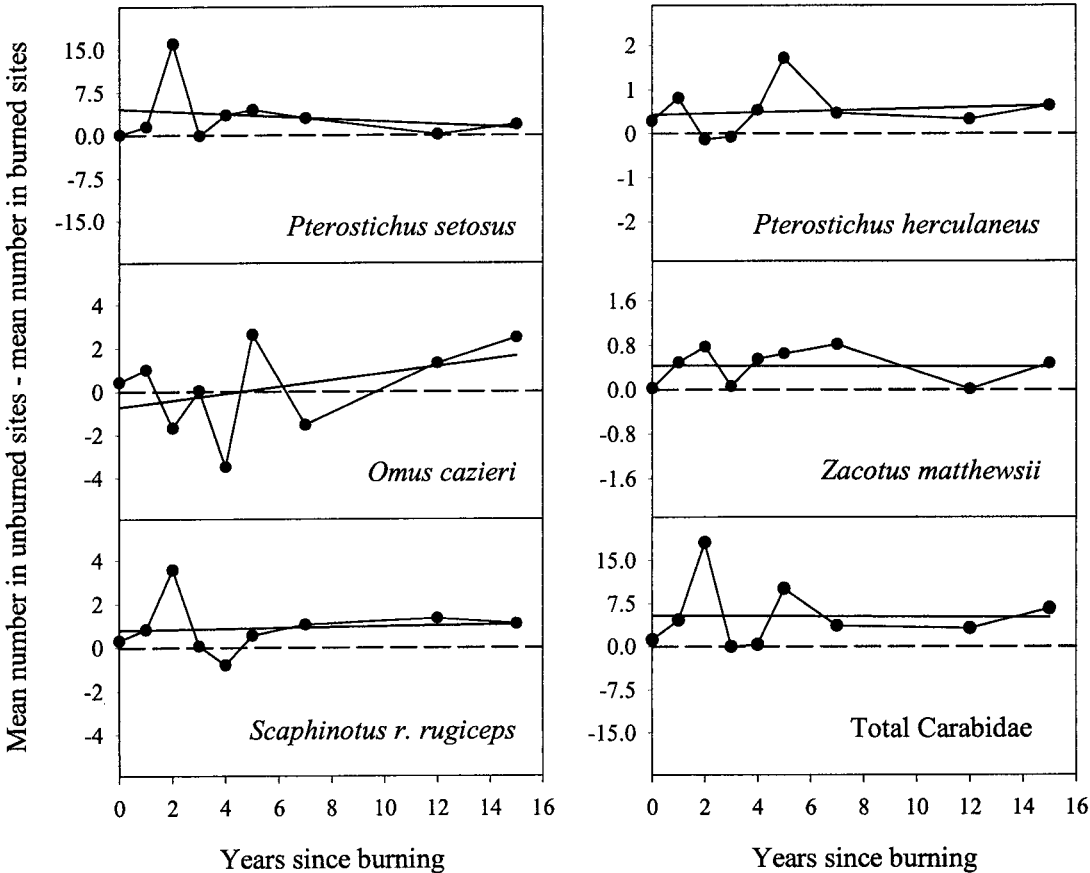

Fig. 2.   Differences in the mean abundance of carabid beetles between paired unburned and burned sites plotted against years since burning. The line through each set of points is a simple regression line illustrating the general direction of points over time.
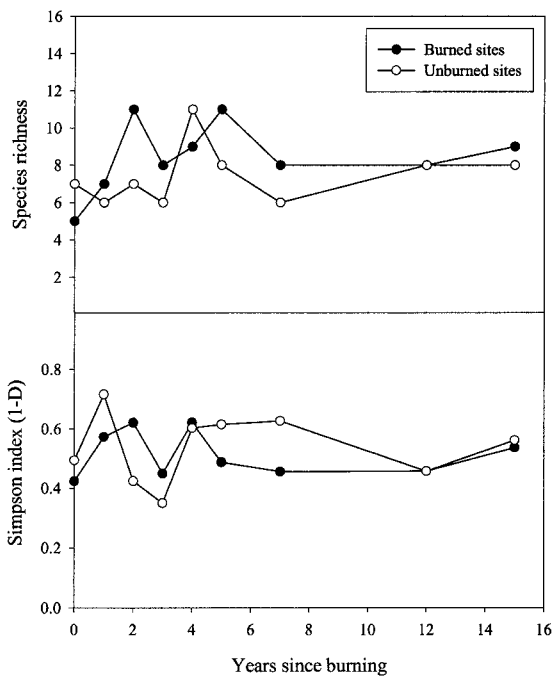
Fig. 3. Species richness (top) and diversity (bottom) of carabid beetles in burned and unburned sites plotted against years since burning.

cies each comprised <1% of the total and 33 were represented by a single individual. Overall, numbers were similar between sites, with 47.2% collected in burned sites and 52.8% in unburned sites. Of the rare species, 30 were found only in burned sites, 17 only in unburned sites, and 58 were collected in both types of sites. In contrast to numerical dominance, Linyphiidae was the most species-rich family (36 species), followed by Gnaphosidae (18 species), Theridiidae (12 species) and Cybaeidae and Agelenidae (seven species each). The abundant Dictynidae consisted of only two species, with *Blabomma* new sp. comprising 95% of the individuals collected. Nine families were represented by a single species. Spider species richness and diversity were similar between burned and unburned sites with no significant differences found for any of the measurements (P > 0.10; Table 3).

Seven spider families were abundant enough to analyze statistically. Because one or two species were often numerically dominant within a family, the abundance pattern displayed by the family generally mirrored that of the dominant species. Therefore, data are only presented for spider families. The following are the families analyzed, and their dominant species: Dictynidae (*Blabomma* new sp.); Gnaphosidae (*Zelotes* near *viola*); Lycosidae (*Alopecosa kochii*); Antrodiaetidae (*Atypoides gertschi*); Cybaeidae (*Cybaeus* new sp. #3); and Thomisidae (*Xysticus pretiosus*). The species-rich Linyphiidae was also analyzed, but no single species dominated this family.

Seasonal patterns of abundance differed considerably among families, but they were generally consis-

tent between treatments over the course of the study (Fig 4). Gnaphosidae and Thomisidae decreased throughout the season while Dictynidae and Cybaeidae were most abundant during the late September and early October sampling dates. Lycosidae and Linyphiidae were bimodal in abundance, with lowest numbers trapped during August. In contrast, Antrodiaetidae were most abundant during August; an increase in abundance was particularly marked in unburned sites.

The final Poisson regression models comparing burned and unburned sites and the interaction between treatment and time since burning are shown in Table 4. All families showed a significant difference between unburned and burned sites, but the direction of the response varied. Antrodiaetidae, Cybaeidae, Linyphiidae, and Thomisidae were more abundant in unburned sites, while Dictynidae, Gnaphosidae, and Lycosidae were trapped more often in burned sites. No difference was found for total spiders combined. The interaction between treatment and time since burning was less pronounced, however, as significance was only marginal for Dictynidae and Gnaphosidae ($P = 0.048$ and 0.052, respectively). For both of these families, the general trend was for the magnitude of the difference between unburned and burned sites to decrease with increasing time since fire. There was little consistency for either family with time since fire for the five youngest fires, but the size of the difference did decrease in a similar pattern for the four oldest fires (Fig. 5). These results were similar to those found for the carabid beetle *O. cazieri*, in that a high degree of variation occurring during the first 4 yr after fire led to a weak pattern overall. Though no statistical analysis was conducted, a visual representation of species richness and Simpson's index for spiders revealed not apparent pattern over time since burning (Fig 6).

Other Arthropods. Seven taxa other than carabid beetles and spiders were analyzed for differences between unburned and burned areas (Fig. 7). Formicidae was the most abundant group, followed by Thysanura, Orthoptera and Opiliones. Formicidae ($T_s = 1$; $P < 0.01$) were significantly more abundant in burned sites than in unburned sites. Diplopoda was the only taxon more abundant in unburned sites ($T_s = 2$; $P < 0.05$). No differences were found for Thysanura ($T_s = 16$; $P > 0.10$), Orthoptera ($T_s = 20$; $P > 0.10$), Opiliones ($T_s = 12$; $P > 0.10$), insect larvae ($T_s = 22$; $P > 0.10$), and Chilopoda ($T_s = 21$; $P > 0.10$).

Litter Biomass. No difference was found in the grams of litter biomass between burned and unburned sites (mean = 68.81, SE = 8.46 and mean = 67.63, SE = 7.93, respectively; $T_s = 16$; $P > 0.10$).

Discussion

Response to Prescribed Fire. The abundance of specimens captured in pitfall traps can represent either the relative activity or population density of a taxon, or a combination of both these factors (Spence and Niemela 1994). Therefore, in interpreting these data, both changes in density and activity levels of

Table 3.   Feeding guild, total number, and mean ± SE abundance, species richness and diversity of the 25 most frequently trapped spiders in nine paired burned and unburned sites

Family and species	Feeding guild[a]	Total no. trapped	Burned	Unburned
Agelenidae		81[b]	2.8 ± 0.5[b]	6.2 ± 2.4[b]
Novolena intermedia (Chamb. & Gertsch)	Funnel web	62	1.1 ± 0.5	5.8 ± 2.4
Amaurobiidae		133[b]	7.1 ± 1.5[b]	7.7 ± 1.5[b]
Callobius paynei Leech	Hackled band	66	4.4 ± 1.3	2.9 ± 1.2
Zanomys aquilonia Leech	Hackled band	58	2.2 ± 0.9	4.2 ± 0.8
Antrodiaetidae		520[b]	19.2 ± 5.8[b]	38.6 ± 8.6[b]
Antrodiaetus pacificus (Simon)	Trap door	129	4.5 ± 1.5	9.8 ± 2.4
Antrodiaetus pugnax (Chamberlin)	Trap door	32	1.8 ± 1.2	1.8 ± 0.9
Antrodiaetus new sp. #1	Trap door	57	2.8 ± 0.5	3.5 ± 0.9
Atypoides gertschi Coyle	Trap door	280	8.7 ± 3.9	22.4 ± 8.3
Anyphaenidae		24[b]	2.0 ± 0.3	0.7 ± 0.3
Anyphaena pacifica (Banks)	Nocturnal running	24	2.0 ± 0.3	0.7 ± 0.3
Corinnidae		38[b]	2.7 ± 0.7[b]	1.5 ± 0.9[b]
Castianeira thalia Reiskind	Nocturnal running	38	2.7 ± 0.7	1.5 ± 0.9
Cybaeidae		356[b]	10.6 ± 1.5[b]	29.0 ± 5.5[b]
Cybaeina new sp.	Funnel web	79	3.0 ± 0.8	5.8 ± 2.9
Cybaeus new sp. #1	Funnel web	40	0.5 ± 0.4	3.9 ± 1.8
Cybaeus new sp. #3	Funnel web	213	6.0 ± 1.3	17.7 ± 4.0
Dictynidae		440[b]	28.7 ± 4.0[b]	20.2 ± 2.2[b]
Blabomma new sp.	Funnel web	420	27.6 ± 4.2	19.1 ± 2.1
Gnaphosidae		531[b]	39.1 ± 6.8[b]	19.9 ± 7.3[b]
Haplodrassus eunis Chamberlin	Nocturnal running	39	2.6 ± 1.4	1.7 ± 0.7
Zelotes fratris Chamberlin	Nocturnal running	169	11.6 ± 3.3	7.2 ± 2.4
Zelotes maybe *viola* Platnick & Shadab	Nocturnal running	184	14.3 ± 4.4	6.1 ± 3.8
Hahniidae		106[b]	2.2 ± 0.8[b]	9.6 ± 3.1[b]
Calymmaria new sp. #1	Funnel web	61	1.1 ± 0.7	5.7 ± 2.1
Cryphoeca exlineae Roth	Funnel web	28	0.1 ± 0.1	3.0 ± 2.1
Linyphiidae		253[b]	11.7 ± 2.8[b]	16.4 ± 3.8[b]
Ceratinops near *inflatus* (Emerton)	Sheet web	31	1.0 ± 0.4	2.4 ± 0.9
Walckenaeria bifida Millidge	Sheet web	27	0.7 ± 0.4	2.3 ± 1.5
Liocranidae		76[b]	4.0 ± 1.1[b]	4.4 ± 1.0[b]
Agroeca ornata Banks	Nocturnal running	39	1.0 ± 0.4	3.3 ± 0.8
Lycosidae		288[b]	23.3 ± 7.1[b]	8.7 ± 2.3[b]
Alopecosa kochii (Keyserling)	Diurnal pursuit	237	18.4 ± 3.6	7.9 ± 2.1
Pardosa dorsalis Banks	Diurnal pursuit	39	3.8 ± 3.8	0.5 ± 0.6
Thomisidae		472[b]	20.9 ± 9.1[b]	31.5 ± 13.8[b]
Xysticus pretiosus Gertsch	Diurnal ambush	337	12.5 ± 9.1	24.9 ± 14.3
Xysticus montanensis Keyserling	Diurnal ambush	108	6.6 ± 1.1	5.4 ± 2.6
Other species		644	39.3 ± 6.0	32.2 ± 3.8
Total spiders		3,441	180.4 ± 28.5	201.9 ± 28.2
Species richness (S)			38.44 ± 1.46	36.89 ± 0.90
Simpson Index (1-D)			0.81 ± 0.01	0.80 ± 0.02
Berger-Parker Index (1/d)			5.52 ± 0.48	6.06 ± 0.52
Shannon-Wiener Index (H′)			2.00 ± 0.04	1.94 ± 0.70

[a] Feeding guild placement based on Post and Riechert (1977) and McIver et al. (1992).
[b] Numbers total values for each family. This number may be greater than the sum for the species listed because less common species are not listed in the table.

macroarthropod predators must be considered in response to fire. For instance, a change in habitat that favors increased prey which in turn supports increased predator populations; or a reduction in prey availability leading to fewer but more actively searching predators, would both result in higher trap captures.

Both carabid beetles and spiders showed a significant numerical response to prescribed burning, although responses varied among taxa. For carabid beetles, abundance was clearly lower in burned sites compared with unburned sites. In contrast, the response of spiders was largely split between those families more abundant in burned sites (Gnaphosidae, Dictynidae, and Lycosidae) and those more abundant in unburned sites (Antrodiaetidae, Thomisidae, Cybaeidae, and Linyphiidae). Factors explaining the observed responses to fire are complex, but may be

strongly influenced by changes in the structure of the understory habitat. The expected short-term consequence of burning is a simplification of habitat due to reductions in litter depth or quality, coarse and fine wood debris and small trees and shrubs consumed by the fire. Such changes in habitat structure may influence the ability of arthropods to obtain food and shelter, as well as affect microclimatic conditions necessary for their survival. Phenological patterns may also influence the impact of direct mortality caused by fire.

Studies have suggested that the composition of spider (Uetz 1979, Bultman and Uetz 1982) and carabid beetle (Michaels and McQuillan 1995) communities are influenced by the structure of forest litter. As a measure of litter structure, we found no difference in litter biomass between burned and unburned sites,
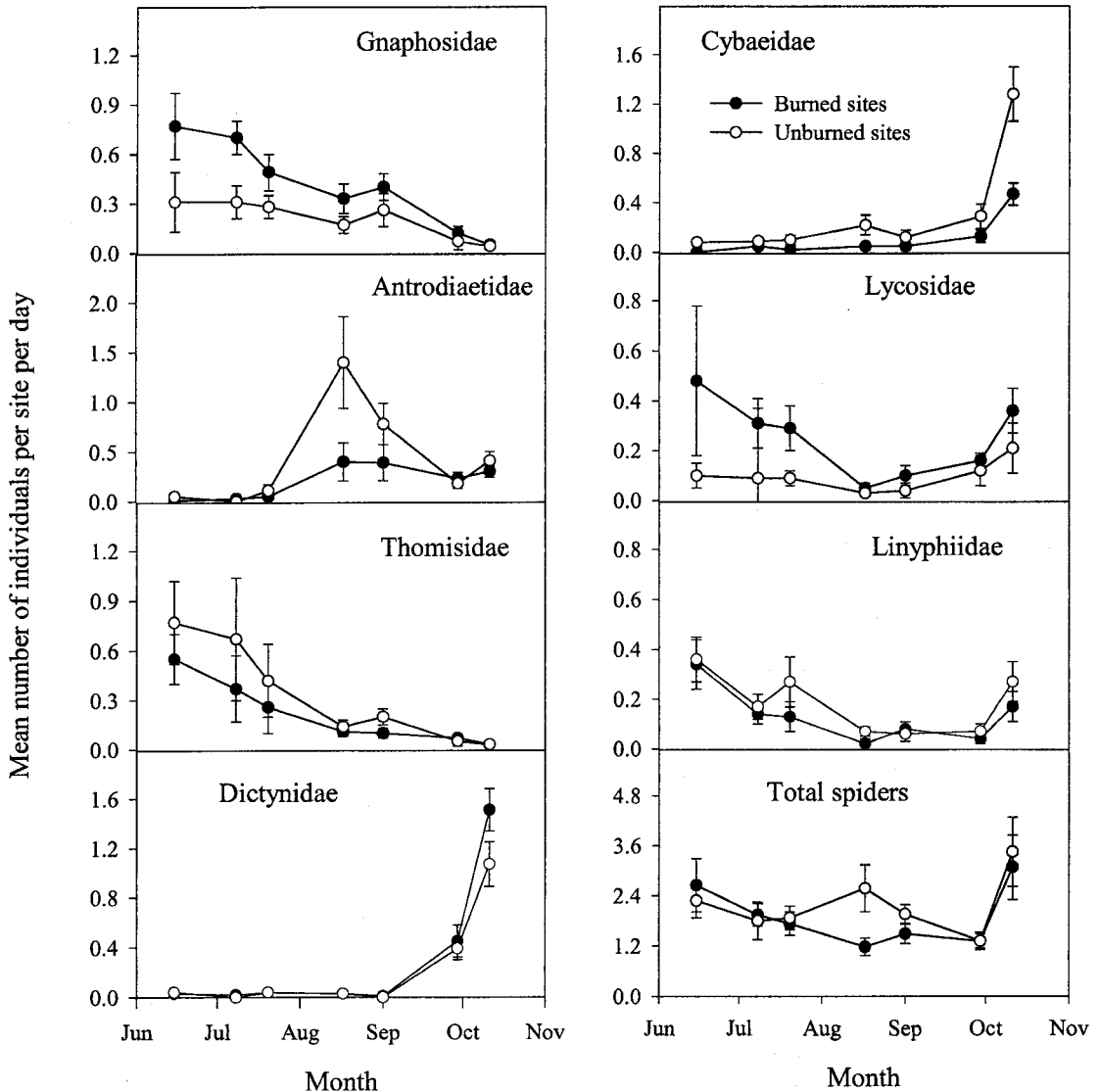
Fig. 4. Mean numbers (±SE) of the seven most abundant families of spiders, and the total number of spiders, in burned and unburned sites on seven sampling dates in 1998 ($n = 9$).

and this factor did not contribute significantly to the regression models used to explain either spider or carabid beetle abundances. The effects of litter consumption were likely confounded by the input of needles that fall from trees killed or stressed by the fire.

For spiders, the method they use to forage for food may have influenced how they responded to fire. Cybaeidae (funnel web spiders), Linyphiidae (sheet web spiders), Antrodiaetidae (trap door spiders), and Thomisidae (ambush spiders), each use different strategies to capture prey, but share a relatively sedentary lifestyle compared with the more active Lycosidae (diurnal pursuit spiders) and Gnaphosidae (nocturnal running spiders). Cybaeidae, Linyphiidae, Antrodiaetidae, and Thomisidae were significantly more abundant in unburned sites than in burned sites

(Table 4). In burned areas, web-building spiders may find structural conditions of the habitat less favorable than in unburned areas if fire reduced the availability of places on which to secure webs (Robinson 1981). In contrast to this pattern, however, the funnel-web building Dictynidae, which are closely related to Cybaeidae, were more abundant in burned sites than in unburned sites. For Antrodiaetidae and Thomisidae, which generally are sit-and-wait predators, fire may have decreased the availability of sites from which they hunt.

The more active hunting spiders, Lycosidae and Gnaphosidae, were collected more often in burned sites than in unburned sites (Table 4). The pursuit style of hunting employed by these spiders may be more productive in burned areas if these sites become

Table 4. Poisson log-linear regression analyses comparing abundance of the seven most common spider families and total spiders in burned and unburned sites

Spider family	Residual deviance	Burned vs unburned						Treatment × time since burning interaction					
		Beta	SE	F	df	P	Direction[a]	Beta	SE	F	df	P	Direction[a]
Antrodiaetidae	3,281.7	0.717	0.205	12.98	1, 113	0.001	Unburned	NA	NA	0.02	1, 106	0.883	None
Cybaeidae	1,561.6	1.132	0.185	43.77	1, 114	<0.001	Unburned	NA	NA	0.47	1, 106	0.494	None
Dictynidae	1,029.0	−0.423	0.252	5.71	1, 113	0.023	Burned	0.050	0.025	4.02	1, 113	0.048	Unburned
Gnaphosidae	1,922.9	−1.073	0.265	2.64	1, 107	0.015	Burned	0.060	0.031	3.85	1, 107	0.052	Unburned
Linyphiidae	1,296.7	0.347	0.172	7.47	1, 113	0.007	Unburned	NA	NA	0.07	1, 113	0.786	None
Lycosidae	2,183.0	−0.927	0.252	14.96	1, 107	<0.001	Burned	NA	NA	0.56	1, 107	0.457	None
Thomisidae	3,082.8	0.436	0.231	4.43	1, 113	0.038	Unburned	NA	NA	0.11	1, 113	0.775	None
Total spiders	4,315.8	NA	NA	2.57	1, 114	0.112	None	NA	NA	0.43	1, 106	0.512	None

A significant interaction between treatment and time since burning indicates that an abundance pattern differed with increasing time since burning. NA, Value not available because the variable was not significant in the final model.

[a] Refers to the treatment having the greatest abundance with increasing time since fire.

more open and structurally simplified after fire. Uetz (1976) also found lycosid spiders to dominate forest communities in which the understory had been simplified by litter removal or compression by flooding.

Adult carabid beetles are all relatively active foragers, but in contrast to hunting spiders, all five species analyzed were more abundant in unburned sites than in burned sites. Our results are similar to those of Holliday (1992) who found fewer individuals in both aspen and conifer forests disturbed by wildfire than in nearby unburned sites. In contrast, Beaudry et al. (1997) found carabid beetles to be significantly more abundant in forest stands recently clearcut, and clearcut and burned, than in an adjacent untreated forest. Although wildfires are generally much more intense than prescribed underburning, the former study is likely more comparable to our system, as clearcutting completely changes climatic conditions as well as altering the understory and litter layer.

The current study was not designed to directly measure prey availability (e.g., active flyers, particularly Diptera and Hymenoptera, were not trapped effectively), but data associated with pitfall trap catches provided insight into potential prey abundances (Fig. 7). We found Formicidae to be significantly more abundant in burned sites than in unburned sites. The greater abundance of hunting spiders in burned sites may have been in response to these insects. McIver et al. (1992) suggest that a dominance of lycosid spiders in recently clearcut sites was influenced by higher numbers of herbivorous prey that had responded to abundant levels of vegetation growing in those sites. Similarly, Formicidae could have been an increased source of prey for hunting spiders after fire, although they also can be competitors (Halaj et al. 1997). In contrast, Collembola within litter were found in significantly greater abundance in unburned sites compared with burned sites (unpublished data). Collembola may be particularly important for the more sedentary spiders and smaller carabid beetles that are more dependent on food within the interstices of litter than on vegetation surfaces (Sunderland et al. 1986, Michaels and MacQuillan 1995). Diplopoda were found in significantly greater abundance in unburned sites, but their value as prey to either spiders or carabid

beetles is unknown. Of the abundant carabid species collected in this study, three (*P. herculaneus*, *P. setosus*, and *S. r. rugiceps*) are considered to be opportunistic foragers, feeding on seeds and fruit as well as arthropod prey (J. LaBonte, personal communication). Burning could have a negative effect on these carabids if supplies of important plant resources such as seeds are destroyed during a fire. Conversely, an omnivorous feeding strategy may help to supplement arthropod prey made scarce because of the effects of fire.

Ameliorative properties of a well-developed understory on microclimatic conditions may also have influenced spider and carabid beetle abundance. Physical properties such as temperature, humidity and moisture content of soil and litter are important factors influencing microhabitat selection for spiders (Uetz 1979) and carabid beetles (Epstein and Kulman 1990).

Life history traits, such as breeding phenology, may influence how fire impacts a species. Most organisms in fire-adapted ecosystems possess adaptations to avoid being killed directly by fire. However, these prescribed burns were conducted in the spring, while wildfires historically occurred in the late summer and fall. Because most of the carabid beetles collected are thought to breed in the spring (J. LaBonte, personal communication), their progeny would have been in the egg or larval stage at the time of burning, and hence may have been particularly vulnerable to fire. *Omus cazieri* was the only carabid beetle not affected by fire, the larvae of this species live within burrows in the soil (200–350 mm deep), and may have had more protection from fire (J. LaBonte, personal communication). Little is known about the ability of adult carabid beetles and spiders to escape fire, but survival would be greatly influenced by the intensity of the fire.

Effect of Fire Over Time. Considering that the overall response to fire was significant for most taxa, it is surprising that there were few significant interactions between abundance and time since burning. We hypothesized that if a significant response to fire was found for a taxon, then the magnitude of the difference would decrease with increasing time since fire, regardless of the direction of the response. It is not
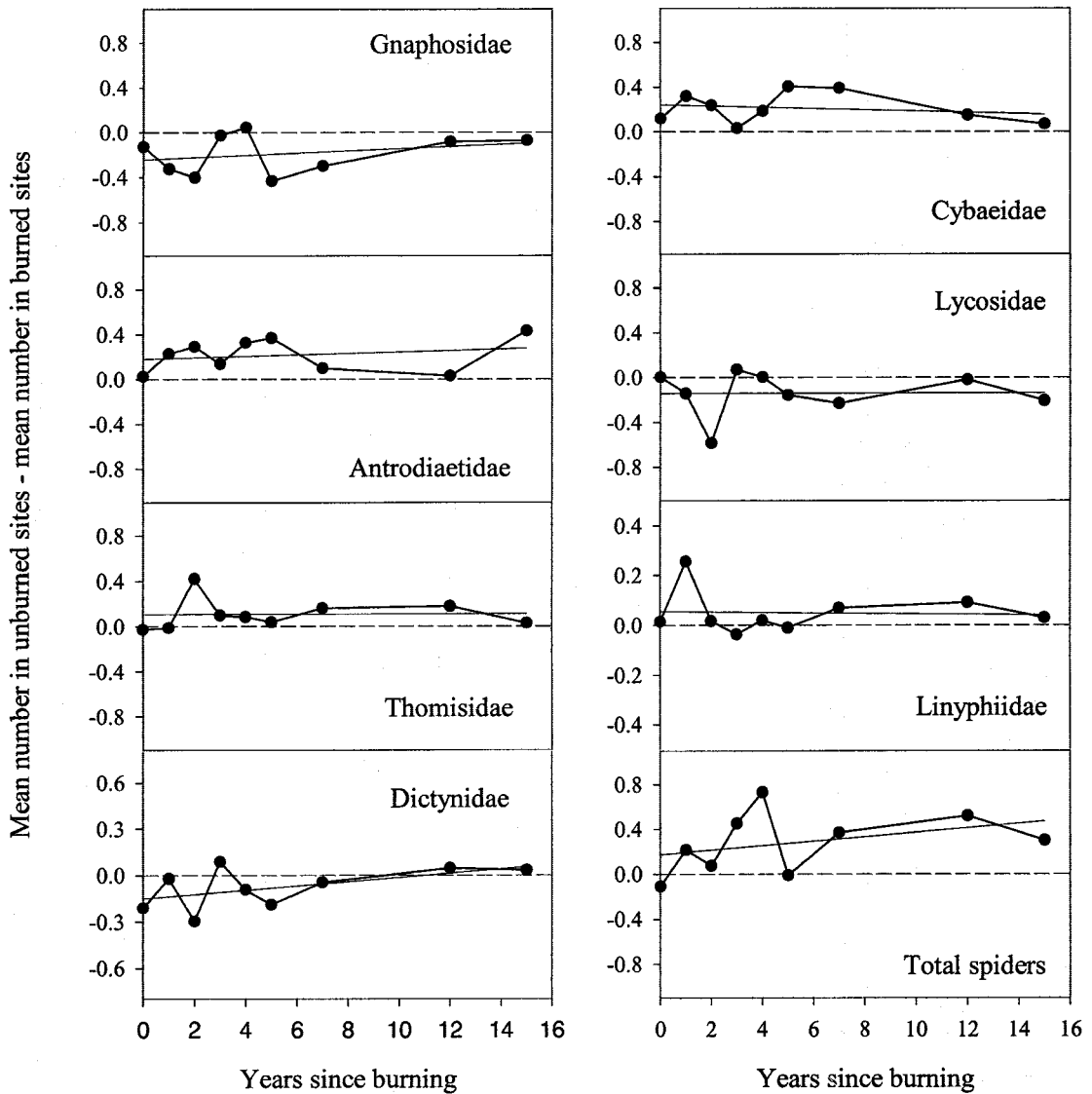
Fig. 5. Differences in the mean abundance of spiders between paired unburned and burned sites plotted against years since burning. The line through each set of points is a simple regression line illustrating the general direction of points over time.

clear why stronger patterns with time were not found, but it is possible that the variability of fire intensities among burn years may have masked patterns. The impact of an older, more intense fire may be greater than that of a younger fire that was less intense. For example, although we expected the largest differences following the 1998 fire, wet and cool weather conditions resulted in a patchy, light intensity fire and relatively small differences between the burned and unburned sites for all taxa analyzed. Data describing fire intensity and its impact on the habitat (i.e., changes in litter structure and herbaceous vegetation) may be necessary to allow effective comparison of fires occurring in different years.

The rate at which spider and carabid beetle populations recover after fire is influenced by both the extent of survival within burned areas and the recolonization abilities of the taxa affected. Because many prescribed burns are spatially heterogeneous and of relatively light intensity, refugia of unburned areas within most sites likely exist. Surviving individuals within these areas may then facilitate reestablishment of populations. For example, lycosid spiders within the genus *Pardosa* have been shown to move >80 m in 100 d (Hallander 1967), easily allowing them to enter burned sites from adjacent unburned areas. In addition, many spider species, in both cursorial and web-building families, use ballooning as a means of dis-
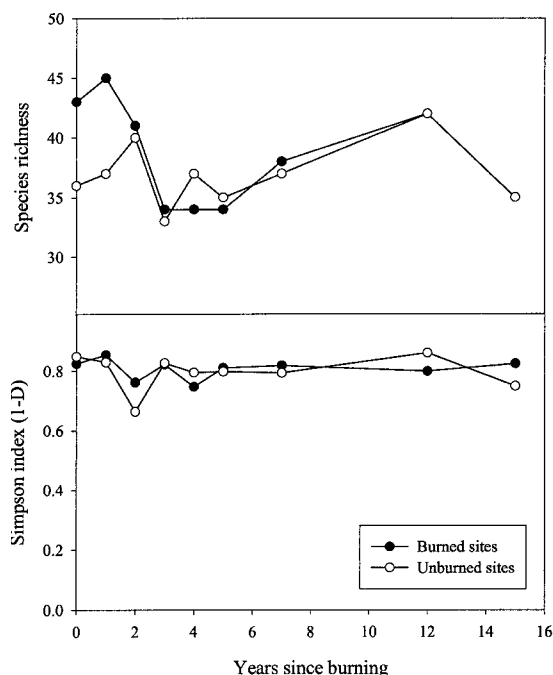
Fig. 6. Species richness (top) and diversity (bottom) of spiders in burned and unburned sites plotted against years since burning.

persal. Many carabid species are able to fly, but all of the common species collected in our study are flightless, which would reduce their ability to recolonize burned areas.

Management Considerations. Forests in southwestern Oregon are managed for a variety of purposes, including habitat for wildlife, areas for recreation,
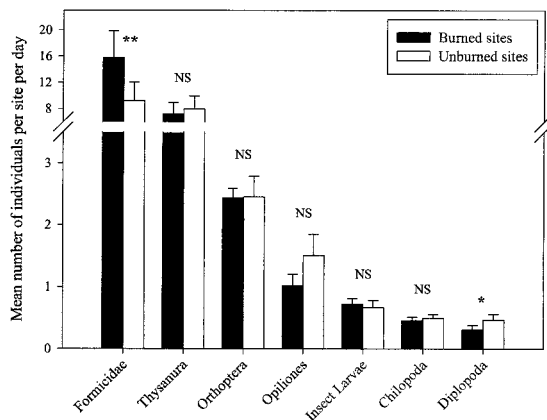

Fig. 7. Mean numbers (±SE) of arthropods other than carabid beetles and spiders collected in burned and unburned sites. Holometabolous insect larvae are comprised mostly of Coleoptera and Lepidoptera. Results of statistical comparison using Wilcoxon's signed-ranks test is shown above paired bars. Levels of significance are as follows: *, $P < 0.05$; **, $P < 0.01$; NS, not significant.

protection of municipal water supplies and production of harvestable timber. Fire, whether natural or prescribed, plays an important role in structuring both forests and arthropod communities in this area. Because many litter arthropods have relatively specific habitat requirements, it is not surprising that prescribed fire influences their community structure and abundance. However, it is important to recognize that decades of wildfire suppression have resulted in heavy fuel accumulations and altered stand structures, leaving much forestland at risk to high intensity wildfire. The current structure of many of these forests differs substantially from historic conditions and often is not in the state desired by forest managers (Brown 2000). Therefore, litter arthropod community structure in unburned areas in our study serves as undisturbed comparisons to burned areas, but may not represent what would occur under desired stand conditions. Ideally, research identifying the effects of disturbance in areas where forests are being actively managed would include the desired future condition, against which all other treatments are compared.

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